

NEW PYGOCEPHALOMORPH CRUSTACEANS FROM THE PERMIAN OF CHINA AND THEIR PHYLOGENETIC RELATIONSHIPS

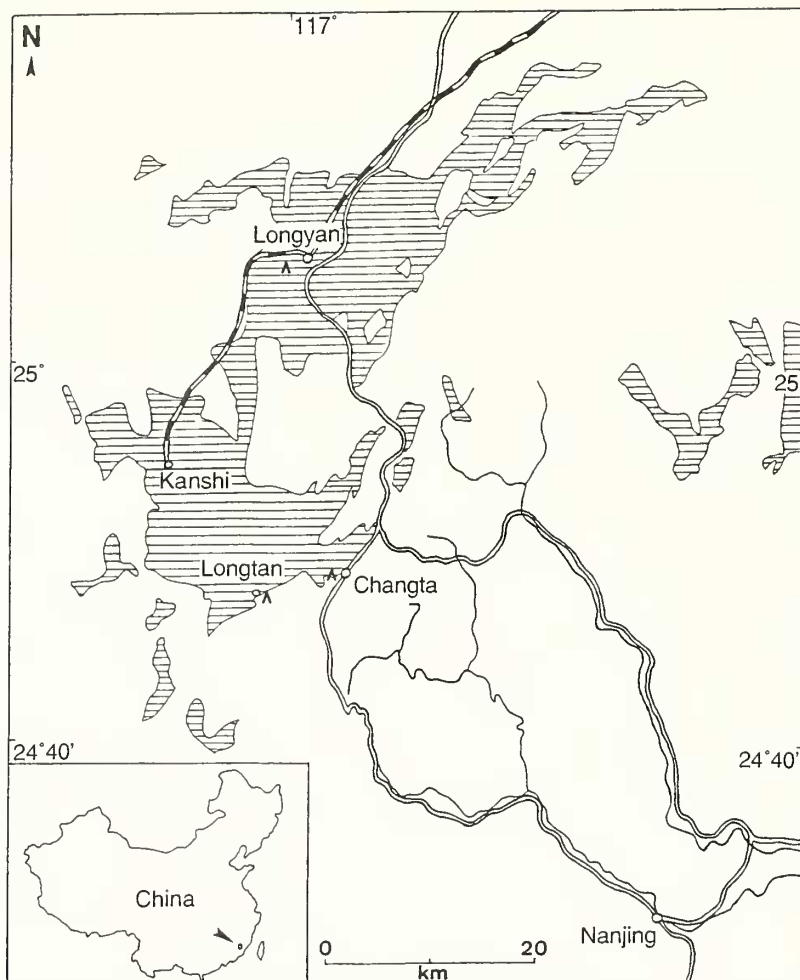
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ABSTRACT. Members of the malacostracan order Pygocephalomorpha are among the most characteristic elements in nearshore marine and freshwater communities in the Carboniferous and Permian of Europe and North America. A new family of pygocephalomorph Eumalacostraca, Tylocarididae, with two new monospecific genera, is described from China, where it occurs in the Early Permian Tungtzeyen Formation of Fujian, and in the Late Permian Lungtan Formation of Hunan. The descriptions of *Fujianocaris bifurcatus* gen. et sp. nov. and *Tylocaris asiaticus* gen. et sp. nov. are based on dorsally preserved isolated carapaces, some showing incomplete abdominal details, but with no complete tail fans. Opinions on the affinities of Pygocephalomorpha to other malacostracans have varied but they are generally regarded as a separate order of 'mysidacean' peracarids. Hitherto the phylogeny of the group has not been considered, and the current family level taxonomy remains rather artificial. A cladistic analysis of fossil and Recent 'mysidacean' and pygocephalomorph crustaceans is presented here which outlines the affinities within the group and holds promise for an eventual natural taxonomy of the Pygocephalomorpha.

LITTLE work has been done on the palaeobiology and taxonomy of fossil Crustacea in China, especially with respect to global biogeography (Shen 1983), with the exception of extensive taxonomic work on conchostracans, which range from the Devonian to the Cretaceous (Shen 1978, 1981, 1984, 1990; Zhang *et al.* 1990). Palaeobiological research has increased in China recently due to the discovery of such important localities as the Cambrian *Lagerstätte* at Chengjiang (e.g. Chen *et al.* 1995a, 1995b), and a result has been the discovery of new crustaceans in Early Permian strata in south-east China. This paper describes the new taxa *Fujianocaris bifurcatus* and *Tylocaris asiaticus*, both apparently belonging to the Pygocephalomorpha. Whilst these new species are only the second reported discovery of Pygocephalomorpha in China (see Shen 1983), members of this order have long been recognized elsewhere as one of the most prominent and striking crustacean groups in late Palaeozoic nearshore marine and freshwater communities, in particular from North America and Europe. However, determination of the phylogenetic affinities of this enigmatic group has remained problematical.

Prestwich (1840) was the first to describe a pygocephalomorph, a carapace from the British Coal Measures; he named it *Apus dubius*, and believed that its affinities might be with the notostracan phyllopod. Later, Huxley (1857) described *Pygocephalus cooperi*, also from the British Coal Measures; in this specimen the ventral aspect of the thorax is preserved, but he did not compare it with *A. dubius*. Salter (1861) realized that the carapace described by Prestwich was not a phyllopod, and erected the genus *Anthropalaemon* to accommodate it and some newly discovered carapace specimens that he ascribed to another species, *A. grossarti*. No-one appreciated at that time that these various taxa had affinities to one another. Indeed, there persisted in the literature an unnatural dichotomous taxonomy: fossils preserving a dorsal view of the carapace were placed in *Anthropalaemon*, while those preserving the ventral aspects of the thorax bore the name *Pygocephalus*. The confusion increased when Woodward (1879) applied the generic name *Necroscilla* to separate abdomina and Salter (1863) placed a tail fan in a separate genus *Diplostylus*.

The generic name *Anthropalaemon* became widely employed for any large lobster-like carapace.



TEXT-FIG. 1. Localities from which *Fujianocaris bifurcatus* and *Tylocaris asiaticus* have been collected, indicated by arrowheads. Shaded areas represent the Lower Permian.

Peach (1883) erected a separate genus, *Pseudogalathea*, for some distinctly ridged forms, and did the same for some other Scottish taxa that he segregated under the genus *Teallicaris*. Brooks (1962) made a major contribution towards resolving the taxonomy of this group. He proposed *Pseudoteallicaris*, for some distinctly decorated taxa, recognized the synonymy of *Pygocephalus* and *Anthrapalaeomon* (former is senior synonym), confirmed the taxonomic status of the North American species *Anthracaris gracilis*, erected *Mamayocaris* for another North American species, and made some assumptions about the supposed higher taxonomic affinities of the pygocephalomorphs. Brooks suggested that one should not compare pygocephalomorphs with phyllopods, schizopods or decapods, as had been done in the past, but placed them in a distinct order, Eocarida, with various other Palaeozoic forms. Finally, Schram (1974a, 1974b, 1979) imposed some order on the species level taxonomy in the group, especially among the British faunas, clarified the issues of thoracopod anatomy that had coloured Brooks' interpretation of the higher taxonomy, and performed a cladistic analysis that advanced a clear hypothesis about the possible

higher affinities of the pygocephalomorphs. In addition, Schram (1978) also recognized another genus in the Permian of Russia, *Jerometichenoria*.

All these discoveries focused largely on 'northern hemisphere' taxa from Laurentia. Nevertheless, another important source of pygocephalomorphs occurs in 'southern hemisphere', essentially Gondwanan, localities. Broom (1931) described a South African species, *Notocaris tapscottii*, and Clarke (1920) first recognized a Brazilian form, *Paulocaris pachecoi*. Later, Beurlen (1931, 1934) expanded on the South American fauna with his erection of *Liocaris* and *Pygaspis*, both again from Brazil. Brooks (1962) synonymized both of these genera with *Paulocaris*, but they have since been resurrected by other authors (e.g. Pinto 1971), reflecting the taxonomic confusion that has marked the history of this group. Unfortunately, these Gondwanan taxa are based on rare and poorly preserved material, making definitive taxonomic assignments difficult. Brooks (1969) set these poorly known, southern hemisphere forms aside as a separate family, Notocarididae, but its only diagnostic character, reduced abdomen flexed under the thorax, clearly does not apply to all southern forms and may merely be an artefact of preservation. The Brazilian *Pygaspis* bear a regular, large, posteriorly directed abdomen (Pinto 1971), and the supposed diagnostic flexure under the thorax is also present on many specimens of northern hemisphere pygocephalomorphs.

In the course of this work, we noted similarities between our two new genera and the Scottish Carboniferous genus *Pseudogalatea*. However, there are palaeobiogeographical implications arising from this, with phylogenetically highly derived animals, with many apomorphic carapace features, arriving at disparate parts of the Palaeozoic world. Whilst we could not preclude this possibility, it caused us to re-examine the total array of anatomical information that could be derived from fossil pygocephalomorphs and possible near relatives, and we performed a cladistic analysis to test more rigorously our initial conclusions on the affinities of the Chinese taxa.

The material used in this study was obtained from the Permian of Fujian Province, south-east China (Text-fig. 1). Most specimens were collected from a coal mine in the village of Changta, Nanjing County, in the third member of the Early Permian Tungtzeyen Formation (one specimen has also been reported from an equivalent horizon at Longtan village, Yongdin County, Fujian (Zhu 1990, pl. 21, fig. 15)). One specimen was found at each of the following: Xihushan, Longyan County, Fujian Province, Early Permian Tungtzeyen Formation; Shitangpu Village, Lukou Town, Zhuzhou City, Hunan Province, Late Permian Lungtan Formation; and an undetermined locality from the Permian of Fujian. This last specimen, due to its uncertain provenance is not considered further. All specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Academia Sinica.

SYSTEMATIC PALAEOLOGY

Class MALACOSTRACA Latrielle, 1802

Order PYGOCEPHALOMORPHA Beurlen, 1930

Family TYLOCARIDIDAE fam. nov.

Diagnosis. Carapace with large falciform rostrum with central groove and papillated margin; prominent mid-dorsal keel, with posterior bifurcation merging with posterior carapace margin; well-developed cervical and rostro-gastric ridges, surrounding papillated rostral ridge; antero-lateral and postero-lateral spines present; heavily thickened carapace margin. Abdomen with medial and one set of lateral ridges on tergites; elongate telson with finely bifurcated tip; endopods and exopods with serrate margins and no diarsis associated with exopod.

Genus FUJIANOCARIS gen. nov.

Derivation of name. From Fujian Province, China.

Type species. *Fujianocaris bifurcatus*.

Diagnosis. Carapace with prominent mid-dorsal keel, bifurcated at both anterior and posterior ends, and pair of prominent lateral keels; carapace margin, rostrum, cervical ridge and keels decorated with papillations, slightly smaller on the carapace margin and rostrum; remainder of carapace smooth; cervical ridges well developed, with shallow cervical grooves; large falciform rostrum with central groove present.

Fujianocaris bifurcatus sp. nov.

Plate 1, figures 1–5; Text-figures 2B, 3A

Derivation of name. From the posterior bifurcations of the telson and the mid-dorsal keel of the carapace.

Holotype. NIGP 126323 A/B; part and counterpart of a carapace and associated abdomen (Pl. 1, fig. 1).

Paratypes. NIGP 126324A-2, 3, NIGP 126327, NIGP 126328, NIGP 126329-1, 2, NIGP 126330-1, 2, NIGP 126331B-2, NIGP 126332A, B, NIGP 126333A/B, NIGP 126334-2, NIGP 126335, NIGP 126336A-1, 2/B-1, 2.

Horizon and locality. No. 25 coal bed, third member of Lower Permian Tungtzezen Formation, Xiangshuping, Changta coal mine, Nanjing County, Fujian Province (Text-fig. 1).

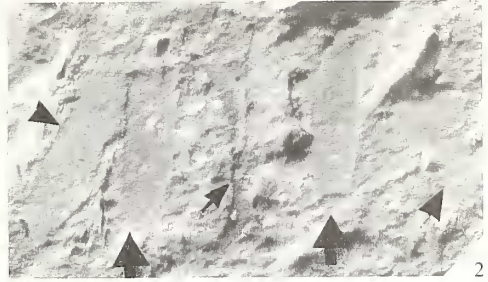
Diagnosis. As for genus.

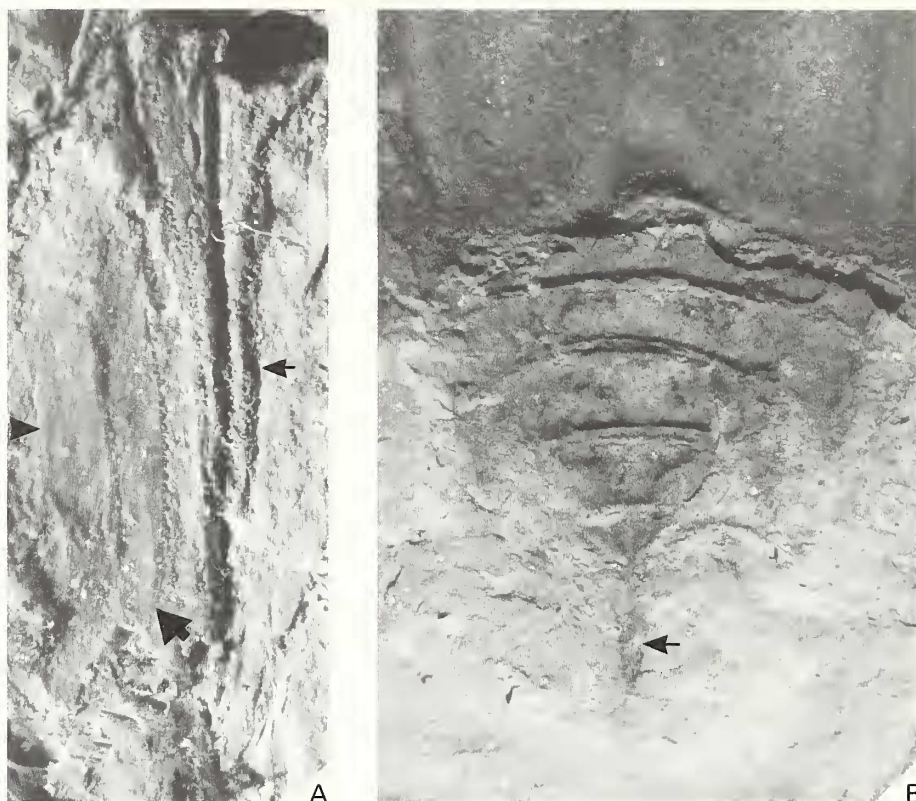
Description. The carapace appears to have been heavily sclerotized. A prominent mid-dorsal keel is present, extending two-thirds to three-quarters its length to the posterior margin (NIGP 126328; Pl. 1, fig. 4). This keel is continuous with a greatly thickened ridge along the posterior, lateral and anterior margins of the carapace. At the immediate anterior end of the medial keel is a pair of antero-laterally directed cervical ridges (in some specimens, these appear to be almost continuous with the keel (NIGP 126330-1; Pl. 1, fig. 3)). These ridges are curved slightly outwards and extend approximately one-third of the distance to the lateral margins of the carapace; they appear to run parallel to what seems to be a set of very shallow cervical grooves (NIGP 126329-1, 2). At its posterior end, the medial keel terminates in a pair of mid-lateral, posteriorly directed spines (NIGP 126323B, NIGP 126331B-2). A pair of lateral keels extends from just posterior of the cervical grooves to the posterior carapace margin, approximately midway between the medial keel and the lateral margin of the carapace (NIGP 126328). These lateral keels extend for approximately the same distance as the medial one. Papillations decorate all keels, more heavily on the medial, and the thickened posterior and lateral carapace margins (NIGP 126330-1; Pl. 1, fig. 3). No branchiostegal spines are present.

The rostrum is long, approximately one-quarter the length of the carapace, and curves slightly ventrally. It is semicircular in cross section, with a dorsal, central groove (NIGP 126330-1, NIGP 126334-2, NIGP 126329-1, 2), and originates from a triangular rostral ridge anterior to the cervical ridges (NIGP 126330-1). The rostral margin and rostral ridge are papillated. There emerges from this rostral ridge a pair of papillated antero-lateral gastric ridges, running approximately parallel to the antero-lateral margin of the carapace (NIGP 126336B-1, NIGP 126329-1, 2). These ridges are wider and more robust laterally than mid-dorsally. At their lateral extent they turn posteriorly, adjacent to the termination of the cervical ridges (NIGP 126330-1, 2). Short,

EXPLANATION OF PLATE 1

Figs 1–5. *Fujianocaris bifurcatus* gen. et sp. nov. 1–2, NIGP 126323A, holotype. 1, $\times 4$; 2, tail fan (small arrow = telson, large arrows = endopods, tailless arrows = exopods); $\times 11$. 3, NIGP 126329-1; $\times 11$. 4, NIGP 126328, $\times 5.5$. 5, NIGP 126322, $\times 5$. 1–3 from the Early Permian Tungtzezen Formation, Changta, Nanjing County, Fujian Province; 4 from the same formation, Xihushan, Longyan County, Fujian Province; 5 from the Late Permian Lungtan Formation, Shitangpu, Lukou, Zhuzhou, Hunan Province.





TEXT-FIG. 2. A, *Tylocaris asiaticus* gen. et sp. nov.; NIGP 126324A; partial tail fan; $\times 14.5$. B, *Fujianocaris bifurcatus* gen. et sp. nov.; NIGP 126334; abdomen and tail fan; $\times 12.5$. Both specimens from the Early Permian Tungtzeyen Formation, Changta village, Nanjing County, Fujian Province (small arrow = telson; large arrows = endopods; tailless arrows = exopods).

rounded, antero-lateral and long, postero-lateral spines are present (NIGP 126323B, NIGP 126327, NIGP 126331B-2, NIGP 126334A-2, 3). A set of broad optic notches is located between the rostrum to the antero-lateral spine.

The abdomen is short, slightly less than one-half the length of the carapace (NIGP 126323A, NIGP 126334-2). Four abdominal segments are exposed (the first two shielded under the carapace), each possessing well-developed pleura with posteriorly-directed processes. Each abdominal tergite possesses a mid-dorsal triangular boss (best developed on the last two pleomeres) as well as a pair of small lateral ridges (NIGP 126332B). The length of the segments remains constant whilst the width decreases markedly in the series, such that the sixth abdominal segment is approximately one-half the width of the third (NIGP 126323A, NIGP 126327, NIGP 126334-2). The telson is narrow and very long, with a length *c.* 2.5 times that of the last abdominal segment (NIGP 126323A, NIGP 126334-2) (Text-fig. 2B). The telson possesses a longitudinal, medial ridge (Pl. 1, fig. 2), whilst its distal terminus appears to form a small fork (NIGP 126323A). The uropods consist of lobate exopods and endopods, the latter with medially serrate margins (NIGP 126323A). No diaresis is noted on the exopods, nor are statocysts visible.

Remarks. The sole specimen (Pl. 1, fig. 5) collected from the Late Permian Lungtan Formation of Shitangpu village, Hunan Province is of particular interest. It is included here in *Fujianocaris bifurcatus*, despite some small differences from other members of this species. In most aspects (e.g. the cervical and gastric ridges and the mid-dorsal keel) it is like other specimens of *F. bifurcatus*, but

TABLE 1. Measurements in millimetres of *Fujianocaris bifurcatus*.

| Specimen | Rostrum length | Carapace length | Abdomen length | Abdominal segment width | | | | Telson length |
|-----------|----------------|-----------------|----------------|-------------------------|------|-----|-----|---------------|
| | | | | 1 | 2 | 3 | 4 | |
| 126322 | > 1.7 | 12.2 | | | | | | |
| 126323A | > 1.3 | 9.3 | 5.8 | 8.5 | 7.4 | 5.9 | 4.5 | 6.7 |
| 126327 | > 3.8 | 15.3 | 11.8 | 10.5 | 9.8 | 8.0 | 6.3 | |
| 126328 | 2.8 | 12.2 | | | | | | |
| 126329-1 | > 1.8 | 8.0 | | | | | | |
| 126329-2 | 1.6 | 6.6 | | | | | | |
| 126330-1 | > 3.0 | 14.0 | | | | | | |
| 126330-2 | | 7.8 | | | | | | |
| 126331B-2 | | 13.3 | | | | | | |
| 126332A | 2.7 | 10.5 | | 6.7 | 5.8 | 4.7 | | |
| 126334-2 | | | 3.75 | 5.3 | 4.75 | 3.2 | 2.7 | > 2.0 |
| 126336-1 | 3.0 | 9.5 | | | | | | |
| 126336-2 | 1.7 | 6.8 | | | | | | |

it lacks the lateral keels, that are characteristic of this species. This specimen is preserved such that there is little contrast between it and the surrounding matrix, making it difficult to determine whether all relevant details of the carapace have been preserved, or whether the absence of these keels is an artefact of preservation. Due to the overall similarities between this specimen and the Early Permian *F. bifurcatus*, it is considered for the time being as an unusual member of this taxon rather than a separate species.

Genus TYLOCARIS gen. nov.

Derivation of name. From the Greek *tylos*, knob, referring to the presence of numerous papillations over the carapace.

Type species. *Tylocaris asiaticus*.

Diagnosis. Carapace with prominent mid-dorsal keel, bifurcated at posterior end, with gastric and cardiac ridges anterior to, and hepatic ridges flanking the anterior end; small papillations highly concentrated on mid-dorsal keel and carapace margin, and more loosely distributed over remainder of carapace; cervical and cardiac ridges well developed; rostrum falciform with central groove; telson long and narrow, with elongate medial ridge and small fork on terminus; a pair of pits on the dorsal surface of each endopod and exopod.

Tylocaris asiaticus sp. nov.

Plate 2, figures 1–3; Text-figures 2A, 3B

Derivation of name. From its discovery in Asia.

Holotype. NIGP 126324 A-1/B; part and counterpart of an incomplete carapace and its associated abdomen (Pl. 2, fig. 1).

Paratypes. NIGP 126325, NIGP 126326A/B, NIGP 126331A/B-1, NIGP 126334-1.

Horizon and locality. No. 25 coal bed, third member of Lower Permian Tungtzeyen Formation, Xiangshuping, Changta coal mine, Nanjing County, Fujian Province (Text-fig. 1).

Diagnosis. As that for genus.

Description. The carapace was probably not heavily sclerotized in life, as suggested by wrinkling of some specimens (NIGP 126326B; see Pl. 2, fig. 2). It possesses a very prominent mid-dorsal ridge, extending two-thirds the length of the carapace from the cervical groove to the posterior margin. This median ridge forks posteriorly and is continuous with a thickened ridge along the posterior margin of the carapace. At the point at which these ridges merge, there is a set of tiny, posteriorly directed processes (NIGP 126326B). The posterior thickened ridge continues along the lateral and anterior margins of the carapace (NIGP 126324A-1). Flanking the anterior end of the median ridge is a pair of highly arched hepatic ridges, with concave surfaces facing inwards (Pl. 2, fig. 2). Immediately anterior to these is a fine cervical groove, which is in turn adjacent to a pair of antero-laterally directed cervical ridges (NIGP 126324A-1/B, NIGP 126331B-1).

A pair of broad optic notches is present between the rostrum and a set of tiny, rounded antero-lateral spines (NIGP 126324-1/B, NIGP 126326B). Papillations are densely concentrated on the medial keel and the posterior and lateral carapace margins (NIGP 126324A-1, NIGP 126325), and this ornament is also distributed over the central portion of the carapace, becoming less densely aggregated near the lateral margins (Pl. 2, figs 1–2). No branchiostegal serrations on the lateral margins are present.

The rostrum is long, one-quarter to one-third the length of the carapace. It is slightly falciform, is an extension of the papillated mid-dorsal rostral ridge (NIGP 126331A/B-1), and possesses papillations along its margin. A pair of narrow, weakly developed, antero-lateral ridges emerges from the anteriormost region of the rostral ridge. These extend posteriorly and laterally from the rostral ridge to the cervical groove (NIGP 126331B-1). The carapace bears a pair of short, rounded, antero-lateral spines lateral to the optic notch and a pair of well-developed postero-lateral spines (NIGP 126324B, NIGP 126326B). One specimen (NIGP 126324A/B; Pl. 2, fig. 1) possesses what appear to be dislocated, regularly segmented antennal fragments near the anterior end of the carapace.

The abdomen is approximately the same length as the carapace. Five abdominal segments are exposed, which possess posteriorly pointed pleura. Segment width decreases whilst length increases distally along the abdominal series, such that the sixth abdominal segment is approximately one-half the width but twice the length of the second segment (NIGP 126324A-1). Each of the tergites bears a broad, triangular medial ridge, as well as a pair of narrow, longitudinal lateral ridges (NIGP 126325; Pl. 2, fig. 1). The elongate and narrow telson appears to terminate in a finely forked tip (NIGP 126331A). It is longer by approximately one-third than the final abdominal tergite, and carries a narrow medial keel running its entire length. Two specimens each show what may be a single caudal furca, occurring at approximately the middle (NIGP 126331A) and near the end (NIGP 126323A-1) of the telson. A pair of lobate uropods, possibly distally pointed, are present, the endopod possessing serrate margins (NIGP 126324A-1; Text-fig. 2A). A diarsis is not visible on the exopods. One specimen (NIGP 126325; Pl. 2, fig. 3) exhibits a pair of small pits along the dorsal midline of the exopods and endopods. Statocysts are not seen.

Remarks. There is one anomalous specimen (NIGP 126326 A/B; Pl. 2, fig. 2), which possesses, immediately anterior to the cardiac groove, two sets of three well-developed spines/nodes instead of cardiac ridges, with spine/node size decreasing antero-laterally. It is slightly deformed, but appears to be considerably wider (length/width *c.* 0.8) than the others (length/width *c.* 1.3 in undeformed specimens). Despite these differences, with the small sample it is considered here to be an unusual member of this taxon, and is perhaps an example of sexual dimorphism; more material might demonstrate that it is a different species.

EXPLANATION OF PLATE 2

Figs 1–3. *Tylocaris asiaticus* gen. et sp. nov. 1, NIGP 126324A; $\times 5$; 2, NIGP 126326A; $\times 5$; 3, NIGP 126325; $\times 10.75$ (arrows = pits). All from the Early Permian Tungtzeyen Formation, Changta village, Nanjing County, Fujian Province.



TABLE 2. Measurements in millimetres of *Tylocaris asiaticus*.

| Specimen | Rostrum length | Carapace length | Abdomen length | Abdominal segment width | | | | | Telson length |
|-----------|----------------|-----------------|----------------|-------------------------|-----|-----|-----|-----|---------------|
| | | | | 1 | 2 | 3 | 4 | 5 | |
| 126324A-1 | | ~ 16 | 14.0 | | 7.0 | 5.7 | 5.0 | 4.2 | ~ 6.5 |
| 126325 | | | 9.2 | | 5.4 | 4.6 | 3.8 | 2.7 | ~ 5.3 |
| 126326 | 2.7 | 7.6 | | | | | | | |
| 126331A-1 | 2.9 | 8.0 | 6.3 | | | 3.3 | 2.7 | 1.8 | |
| 126334-1 | 2.7 | 9.6 | | | | | | | |

METHODS

A data matrix based on 33 morphological characters from 31 taxa (Table 3) was created using MacClade 3.01. Taxa were chosen based on several criteria. All 18 known pygocephalomorphs were included, with most data derived from the literature. Some information on British pygocephalomorphs was obtained from examination of material at the Hunterian and Kelvingrove museums in Glasgow, the National Museum of Scotland in Edinburgh, and the British Geological Survey in Keyworth.

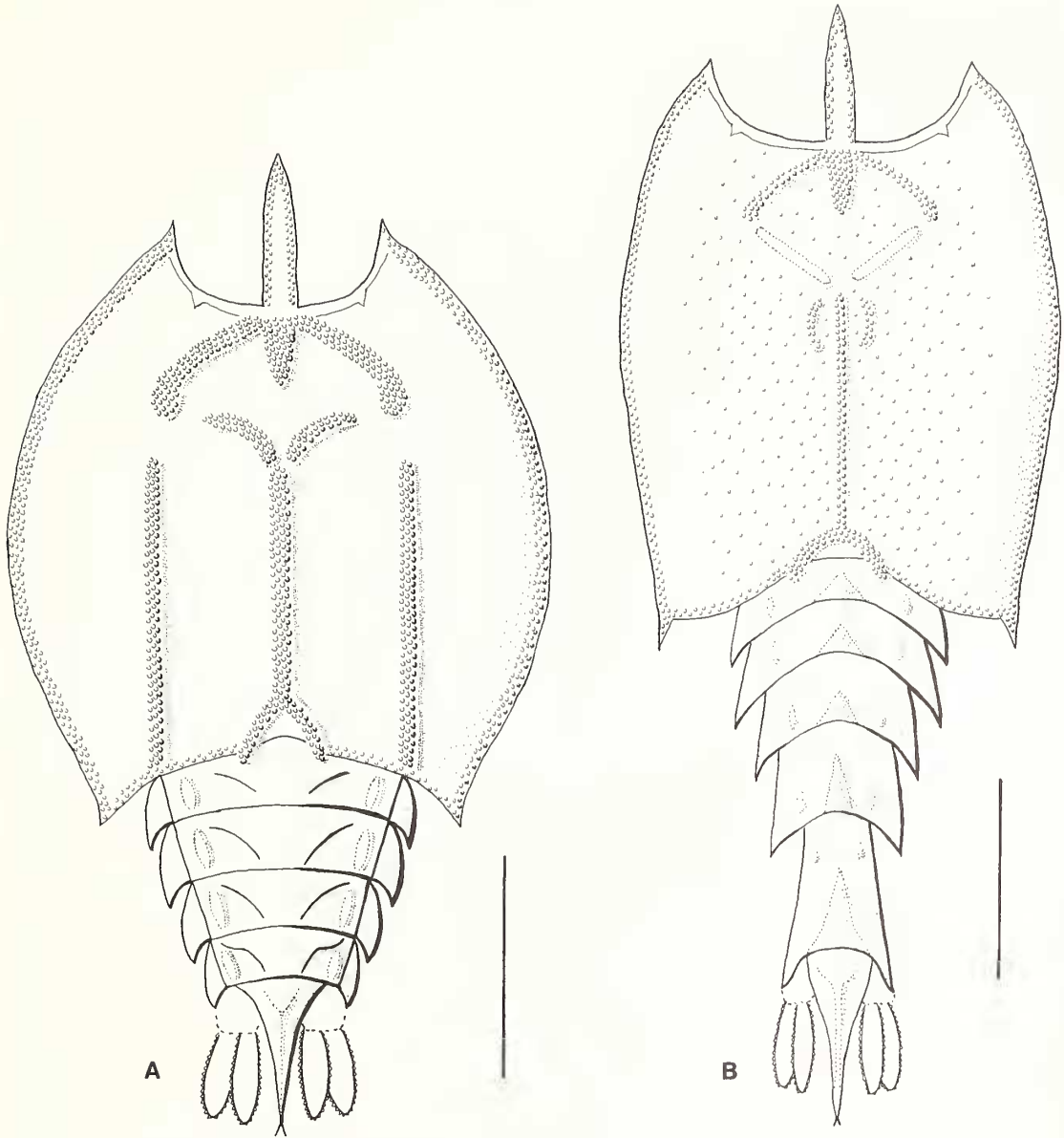
PAUP 3.1.1 was used to perform a cladistic analysis of this matrix. Heuristic searches were the only practical option, due to the large size of the matrix and the high number of unknowns within it. After an initial unweighted analysis of the matrix, a successive reweighting option was employed, in which the unweighted matrix underwent a heuristic search and was then reweighted using the rescaled consistency index (RCI). This was in turn followed by another heuristic search, and so on until there was no further reduction in the minimum tree lengths obtained. This method provided a set of the most parsimonious trees for a matrix in which the most 'important' characters are granted the highest influence on the outcome of the analysis (see Table 4).

Representative recent mysidacean and lophogastrid taxa were included in this analysis, as well as all known fossil mysid forms, to determine whether the new Chinese species were more closely associated to the similar mysidacean/lophogastrid forms than to the pygocephalids. A hypothetical ancestor was used as an outgroup, scored with zeros for all character states – a so-called Lundberg rooting. Whilst such a procedure is not regarded as an ideal solution to the outgroup problem, it proved useful in this analysis as there was no clear choice in the selection of an outgroup: the most obvious choice would be the mysids and lophogastrids, but since these taxa were actually included in the analysis, their use as outgroups would heavily bias the results.

It is important to note that several alternative options were explored in these cladistic analyses, including the exclusion of certain 'problematical' taxa (i.e. *N. tapscotti*, and both *Pygaspis* species) whose positions appeared to be very unstable, the ordering of selected characters, the treatment of the lophogastrid and mysid taxa as outgroup taxa with the exclusion of the hypothetical ancestor from the analysis, and so forth. In each of these cases, the resolution of the tree as well as the consistency index (CI) were reduced, suggesting that the set of trees described here, whilst far from perfect, is probably the best possible based on the currently available information. It is hoped that current work being done in South America by Professor Pinto and his associates (Pinto, pers. comm.) on some of the less well-known pygocephalomorph species, such as *P. pachecoi*, will provide more information on some of the more problematical taxa. This may, in turn, greatly improve the resolution and informational content of analyses of this difficult group.

CHARACTERS

To arrive at our cladistic analysis we assembled a list of 33 features based largely on carapace and tail fan morphology. The commonly incomplete pygocephalomorph specimens forced us to focus



TEXT-FIG. 3. Reconstructions of: A, *Fujianocaris bifurcatus*; B, *Tylocaris asiaticus*. Scale bars represent 5 mm.

on these parts of the exoskeleton, which are those most often preserved and thus provide the majority of the taxonomic characters that are used to define genera and species. The characters and observations on them are listed below, and they include both binary and multi-state features.

1. Hepatic spines absent (0) or present (1). These spines constitute a frequently encountered set anterior to the cervical grooves.
2. Gastric spines absent (0) or present (1). This set of spines characterizes only the monotypic genus *Anthracaris*.

TABLE 3. Data matrix used in the phylogenetic analysis (see Methods and Table 1 for information regarding the identity of the characters).

| Taxon | Character | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|-----------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | | | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | | | | |
| Hypothetical ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | |
| <i>Lophogaster intermedius</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Gnathophausia longispina</i> | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 3 | 0 | 2 | 0 | 0 | | | | |
| <i>Paralophogaster glaber</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Eucopeia unguiculata</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Chalaraspidium alatum</i> | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | ? | 0 | ? | 3 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Ceratolepis hamata</i> | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | | | | |
| <i>Neognathophausia ingens</i> | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | ? | 0 | 0 | 6 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | ? | 2 | 3 | 0 | 1 | 0 | 0 | | | | |
| <i>Peachocaris strongi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 1 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Schimperella beneckeii</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Mysis flexuosa</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| <i>Pygocephalus cooperi</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | | | |
| <i>Pygocephalus dubius</i> | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | | | |
| <i>Pygocephalus aisenvergi</i> | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | | | |
| <i>Teallicaris woodwardi</i> | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | ? | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 1 | | | |
| <i>Pseudogalatea macconochiei</i> | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | ? | ? | 3 | 0 | 0 | 2 | 0 | 0 | 0 | | | |
| <i>Fujianocaris bifurcatus</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | ? | ? | 4 | 1 | 0 | 1 | 1 | ? | 2 | 1 | 1 | 0 | 2 | 1 | ? | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | | | |
| <i>Tylocaris asiaticus</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 1 | 2 | 1 | ? | ? | 6 | 1 | 0 | 1 | 1 | ? | 2 | 1 | 1 | 2 | 1 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | | | |
| <i>Chaocaris chinensis</i> | 0 | ? | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 2 | 1 | 2 | 0 | 0 | | | |
| <i>Anthracaris gracilis</i> | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | | | |
| <i>Pseudoteallicaris caudafimbriata</i> | 0 | 1 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 0 | 0 | ? | ? | 2 | 1 | 0 | 0 | ? | 0 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | | | | |
| <i>Pseudoteallicaris etheridgei</i> | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | | | |
| <i>Pseudoteallicaris palinscari</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 2 | 3 | 0 | 1 | 0 | 0 | 0 | | | |
| <i>Jerometichenoria grandis</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | | |
| <i>Mamayocaris jepseni</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Mamayocaris jaskoski</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Notocaris tapscotti</i> | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | ? | 0 | 0 | 1 | ? | 1 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | ? | 0 | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| <i>Paulocaris pachecoi</i> | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 0 | 0 | ? | 0 | ? | 2 | 0 | 0 | 0 | 1 | 0 |
| <i>Liocaris</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | ? | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | |
| <i>Pygopsis brasiliensis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Pygopsis ginsburghi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 0 | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | |

3. Anterolateral spine absent (0) or present (1). These spines can mark the lateral extent of the optic notch on the anterior margin of the carapace.
4. Postero-lateral 'process' absent (0) or present (1). These variably developed spines can be found at the postero-lateral aspects of the carapace.
5. Branchiostegal spines/serrations absent (0), only on the anterior carapace margin (1) or along the entire carapace margin (2). These distinctive features can ornament either the anterior or the entire lateral margins of the carapace.
6. Mid-dorsal ridge/keel (extending between the cervical groove and posterior carapace margin) absent (0) or present (1). This forms the most prominent component of a complex series of possible grooves and ridges on the carapace of mysidacean-like pericarids.
7. Medio-lateral spines absent (0) or present (1). A set of spines on the posterior margin of the carapace just lateral to the mid-dorsal ridge or keel.
8. Cervical groove whole (0), split (1) or strongly posteriorly directed (2). This is the principal groove

TABLE 4. Final results of the Rescaled Consistency Index (RCI) reweighting of the characters used in this analysis.

| Character | Final weight |
|--------------------------------------|--------------|
| 1 Hepatic spines | 1000 |
| 2 Gastric spines | 133 |
| 3 Anterolateral spine | 97 |
| 4 Posterolateral 'process' | 200 |
| 5 Branchiostegal spines/serrations | 444 |
| 6 Mid-dorsal keel | 58 |
| 7 Medio-lateral spines | 1000 |
| 8 Cervical groove | 111 |
| 9 Cervical constriction | 100 |
| 10 Marginal thickening | 1000 |
| 11 Carapace papillations | 200 |
| 12 Branchiostegal inflation | 1000 |
| 13 Telson lobe number | 389 |
| 14 Telson spine | 267 |
| 15 Telson l/w ratio | 300 |
| 16 Telson medial ridge | 400 |
| 17 Telson terminal process | 400 |
| 18 Telson terminus | 429 |
| 19 Uropod margin | 1000 |
| 20 Uropod diarsis | 100 |
| 21 Abdominal pleurae | 81 |
| 22 Abdominal medial keel | 63 |
| 23 Abdominal lateral keel | 63 |
| 24 Length of sixth abdominal segment | 127 |
| 25 Abdominal posterior narrowing | 389 |
| 26 Abdominal segments visible | 250 |
| 27 Sternal field | 571 |
| 28 Primary lateral keels | 286 |
| 29 Secondary lateral keels | 563 |
| 30 Tertiary lateral keels | 1000 |
| 31 Rostral keel | 156 |
| 32 Cervical ridge | 1000 |
| 33 Rostro-gastral ridge | 1000 |

on the carapace of these crustaceans and stands in contrast to the more complex series of grooves seen on the carapace of decapod eucarids.

9. Constriction of carapace margin at cervical groove absent (0) or present (1).

10. Massive thickening of carapace margin absent (0) or present (1). This forms distinctive structures along the margin.

11. Surface papillations on the carapace absent (0), restricted to specific regions of carapace (1), covering entire carapace (2) or merged to form texture/sculpturing (3). A multi-state feature typically useful in distinguishing between pygocephalomorph species.

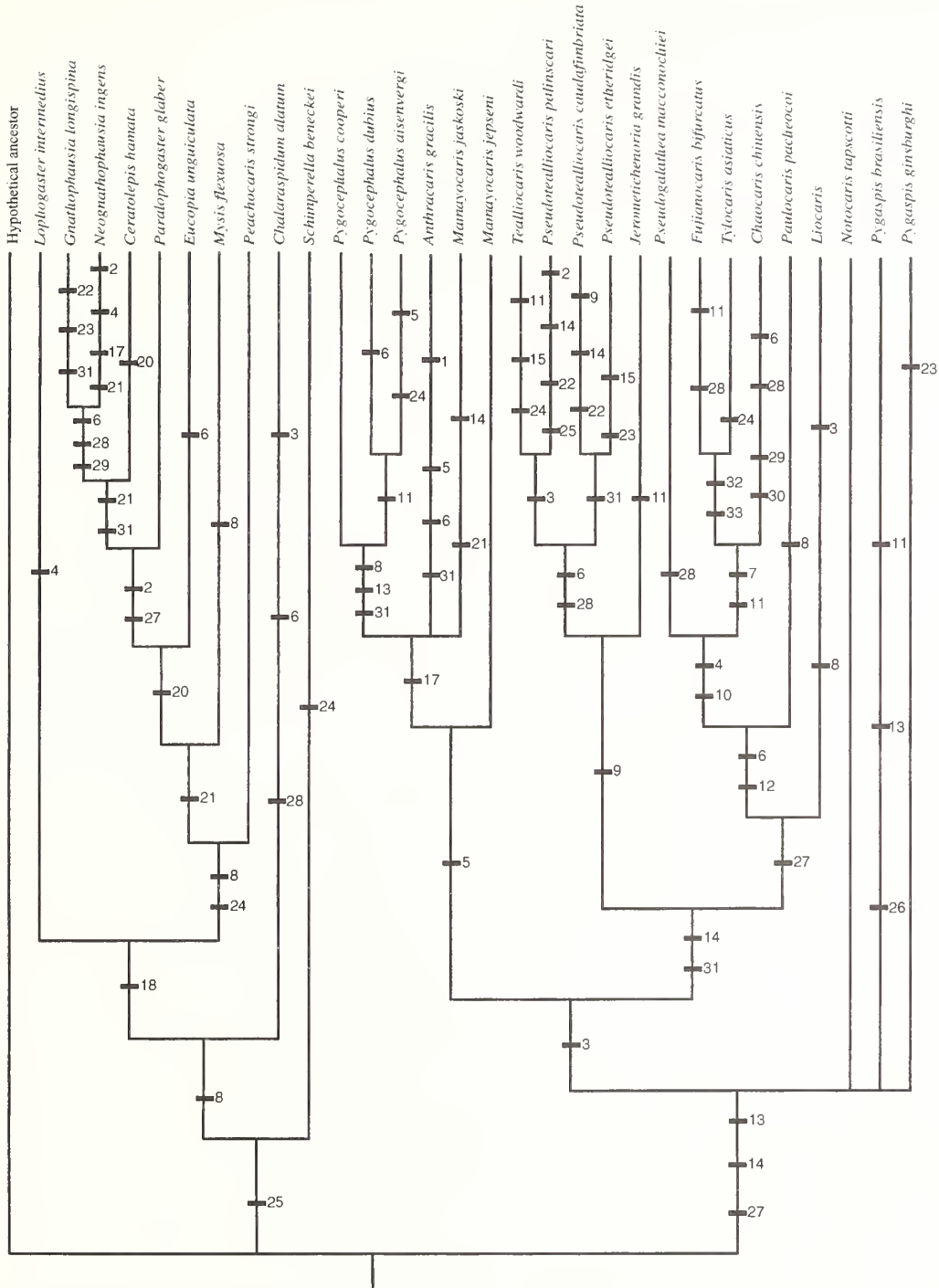
12. Branchiostegal inflation absent (0) or present (1). It is difficult to categorize just what this feature represents. It is well developed in several genera. One could assume it bears some relationship to the possible development of gills in the branchiostegal chamber, but this cannot be easily confirmed in the fossils. It might also bear some relationship to streamlining necessary to facilitate surface flow over the thoracic region of the body.

13. Telson lobe/furca number zero (0), one pair (1) or two pairs (2). This and the following five characters often form a most coherent set of features for generic diagnoses in the order.
14. Telson spine absent (0), rounded (1) or pointed (2).
15. Telson length/width ratio < 0.5 (0), 0.51–1.0 (1), 1.01–1.5 (2), 1.51–2.0 (3), 2.01–2.5 (4), 2.51–3.0 (5), > 3.01 (6).
16. Telson medial ridge absent (0) or present (1).
17. Telson terminal process absent (0) or present (1).
18. Telson terminus whole (0) or forked (1).
19. Uropod margins straight (0) or serrate (1).
20. Uropod diarsis absent (0) or present (1).
21. Abdominal pleurae absent (0), gently rounded (1) or angular (2). Insofar as they are preserved, decorative features of the abdomen (here and in the succeeding characters) can help to delineate species.
22. Abdominal medial keel/ridge absent (0) or present (1).
23. Abdominal lateral keels absent (0) or one pair (1).
24. Length of sixth abdominal segment same as fifth (0), slightly longer than fifth (1) or much longer than fifth (2).
25. Abdominal posterior narrowing: none (0) slight (1) or great (2).
26. Abdominal segments visible: six (0) or one or two covered (1). This feature actually reflects the degree of posterior development of the carapace. Typically the carapace covers only the thorax, but in some instances it extends backwards to cover the anterior part of the abdomen.
27. Sternal field narrow (0), wide and triangular (1) or wide and rectangular (2). This feature is not always evident, unless the ventral part of the thorax is preserved. It appeared (e.g. Schram 1986) that essentially only two forms of thoracic sternite field prevailed: narrow, with little development of sternites; or triangular, with narrow sternites anteriorly and wider ones posteriorly. In examination of some of the pygocephalomorphs from Brazil, it became clear that the observations of Pinto (1971) concerning wide anterior sternites on the thorax to form a more rectangular field have great value. Whilst this feature is unknown in many pygocephalomorph genera at present, we suspect that as more information becomes available this may prove to be a very important character for sorting higher relationships in the group.
28. Primary lateral keels absent (0), medio-lateral (1), gastro-lateral (2) or postero-lateral (3).
29. Secondary lateral keels absent (0), free (1), postero-lateral (2), close to lateral margin (3) or 'fused' with lateral margin (4).
30. Tertiary lateral margin absent (0) or present (1).
31. Rostral keel absent (0), not reaching cervical groove (1) or reaching cervical groove (2).
32. Cervical ridge absent (0) or present (1).
33. Rostro-gastral ridge absent (0) or present (1).

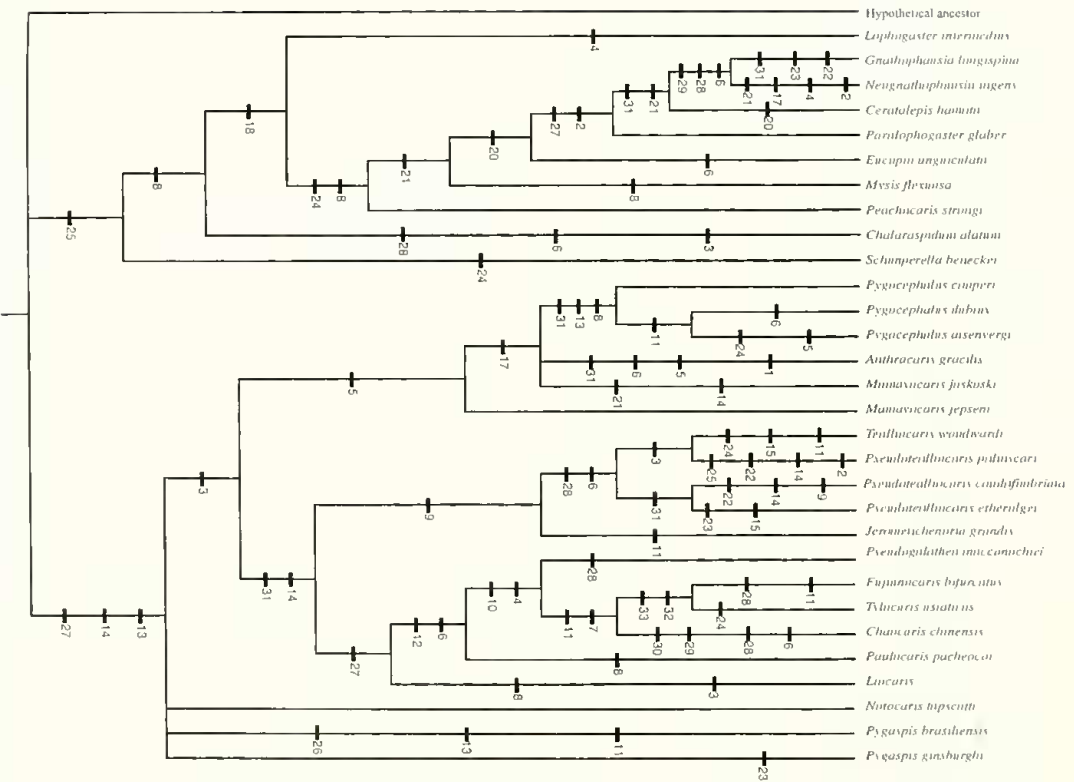
RESULTS

For the initial, unweighted analysis, a total of 30 most parsimonious trees with a length of 129 steps was found, with a CI of 0.411. These trees, whilst showing some trends for specific groups in the analysis did not provide sufficient resolution to deduce relationships for all taxa involved, and thus we employed the use of the reweighting methods discussed above. This successive weighting regime provided a total of 15 most parsimonious trees of length 132, with a CI of 0.402. A 50 per cent. majority rule tree for these trees is shown in Text-figure 4.

Several interesting relationships emerged from this analysis. First, the recent and fossil mysids plus the recent lophogastrids form a distinct (if somewhat confused) clade, even when not specifically treated as an outgroup in the analysis. Within the pygocephalomorph 'ingroup', several distinct clades are evident which show considerable overall support for some of the taxonomic divisions outlined by Brooks (1962). As seen in the tree in Text-figure 4, the three species of



TEXT-FIG 4. Strict consensus tree of the 15 trees obtained from an analysis incorporating successive reweighting of a pygocephalomorph and lophogastrid data set, using a hypothetical ancestor as outgroup. Character state changes are plotted (see Methods section for further details).



TEXT-FIG. 4. Strict consensus tree of the 15 trees obtained from an analysis incorporating successive rewighting of a pygocephalomorph and lophogasterid data set, using a hypothetical ancestor as outgroup. Character state changes are plotted (see Methods section for further details).

Pygocephalus form a monophyletic group with *Anthracaris* and both species of *Mamayocaris*. This closely reflects Brooks' (1962) taxonomic scheme, in which *Anthracaris* and *Mamayocaris* are included with *Pygocephalus* in the family Pygocephalidae. One major disagreement with Brooks (1969) is the unification of *Teallicaris* with the three species of *Pseudoteallicaris* to form a monophyletic clade; he had placed the latter in Pygocephalidae and the former in Teallicarididae. Thus, Brooks' generic distinction between *Teallicaris* and *Pseudoteallicaris* may be an unnatural taxonomic separation. His familial separation of these genera is certainly suspect. *Jerometichenoria* is united by this analysis with this teallicaridid clade, suggesting that the family Jerometichenoriidae, proposed by Schram (1978), may also be unnecessary.

A close relationship seems to exist between the three Chinese forms, *Fujianocaris* and *Tylocaris* and the Carboniferous *Chaocaris*, and the British *Pseudogalatheia*, and this may also extend to the problematical South American genera *Paulocaris* and *Liocaris*. This is perhaps the most interesting relationship to emerge from this analysis, as it could indicate taxonomic and palaeobiogeographical relationships between these geographically widely separated taxa. This result also contrasts with Brooks' (1962) interpretation, in that his placement of *Pseudogalatheia* with *Teallicaris* in Teallicarididae is not supported by this analysis. In addition, Brooks placed *Paulocaris* in Notocarididae with *Notocaris*, another association that does not appear to be supported by this analysis. Both the *Pygaspis* species and *N. tapscottii* occur basally in the pygocephalomorph 'clade', with no clear associations to any of the three major pygocephalomorph clades expressed in the analysis. We hope that a more adequate understanding of the anatomy of the southern hemisphere species will resolve the polytomies in this part of the tree, and allow us to address definitively the issues of pygocephalomorph classification.

DISCUSSION

Age

Beds of the Tungtze Formation containing *Fujianocaris bifurcatus* also contain several other taxa, including plants, conchostracans, bivalves, brachiopods, gastropods, ammonoids, fusulinids and crinoids. These taxa collectively are the basis for the assignment of an Early Permian age for the Tungtze Formation (Sheng *et al.* 1982).

Morphology

At the outset of this study, it was assumed that the two new species were members of the extinct Carboniferous/Permian order Pygocephalomorpha, based on overall morphology and similar time ranges. However, we also considered that they might be related to Recent mysids or, more likely, Recent Lophogastrida. There is a great number of morphological similarities between the latter and the Pygocephalomorpha. They have both been considered as sub-orders of the Mysida, and were elevated to the status of separate orders by Schram (1984). The main distinguishing characters for the Pygocephalomorpha are the presence of a triangular field of sternites on the ventral surface of the thorax and the development of a complex tail fan, including at least one pair of caudal furcae associated with the telson (Schram 1986). Since none of the specimens described here shows either ventral preservation or a complete tail fan, these unfortunately could not be used.

Important characters that distinguish these new species from the morphologically similar pygocephalomorph *Pseudogalatheia* are: the complex cervical and rostro-gastric ridges; the medial ridge of the telson in the tylocaridids; and the highly elongated postero-lateral spines of *Pseudogalatheia*. *Pygocephalus*, another pygocephalomorph to which *F. bifurcatus* and *T. asiaticus* could be compared (Brooks 1962, 1969), is distinguishable from the tylocaridids by the absence of antero-lateral serrations on the carapace margin, the presence of a medial ridge on the telson, and the presence of carapace ridges. A third pygocephalomorph genus, *Chaocaris*, occurs in China (Shen 1983) and has several similarities to the tylocaridids, but is distinguished by its possession of a set of mid-lateral carapace keels, the absence of a medial carapace keel, and an elongate, narrow rostral

ridge extending from the anterior end of the carapace to the cervical ridge. The taxonomic placement of *Chaocaris* with the pygocephalomorphs is uncertain, as this taxon is based on a single carapace.

T. asiaticus and *F. bifurcatus* also show similarities to mysidacean species known from the fossil record, in particular *Schimperella benecke* and *Peachocaris strongi*. *S. benecke* can be distinguished by its six exposed abdominal somites and its possession of a truncate telson that is shorter than its associated uropods (Hessler 1969), and *P. strongi* by its rounded abdominal pleurae, the exposure of all six abdominal somites, and the presence of large, rounded postero-lateral lappets on the carapace (Brooks 1962).

One important morphological character that suggested to us a possible relationship between *F. bifurcatus* and *T. asiaticus* and the lophogastrids instead of the pygocephalomorphs is the apparent presence of a bifurcation at the terminal end of the telson, resembling a pair of terminal spines. This is a common occurrence in the order Lophogastrida but is generally absent among pygocephalomorphs. This is, however, an uncertain character at best, due to the usually poor nature of preservation of the tail fan in these animals.

Associated faunas and ecology

Specimens of *Tylocaris asiaticus* and *Fujianocaris bifurcatus* were collected from three different localities in south-east China: most are from the Early Permian Tungtze Formation at Changta, Fujian, which comprises alternating thin beds of grey to dark grey, fine-grained quartz sandstone and siltstone, interbedded with mudstone and coal beds. The accompanying flora and fauna includes plants (*Gigantonoclea fukiensis*, *Sphenophyllum sino-coreanum*, *Pecopteris (Rajahia) rigida*, *P. helitelioides*, *Sphenopteris tenuis*, *Asterophyllites longifolius*, *Lobatannularia lingulata*, *Gigantopteris dictyophylloides*, *Compsopteris* sp., and *Cordaites* sp.), bivalves (*Bakevellia ceratophaga*, *Wikingia elegans*, *Vosellina* aff. *yunnanensis*, *Astartella* cf. *ambiensis*, *Stuchburia* sp. and *Palaeoneilo* sp.), brachiopods (*Cathaysia* sp., *Neoplicatifera* sp., *Linoproductus* sp., *Lingula* sp. and *Pygnochonetes* sp.), gastropods (*Cyclozyga* sp., *Baylea* sp. and *Bellerophon* sp.), ammonoids (*Altudoceras* sp. and *Schouchangoceras* sp.), crinoids (*Cyclocyclicus quinquelobus*) and unidentified insect wing fragments.

The flora at these south-east Chinese localities may represent the Late Palaeozoic Cathaysian flora (see Zhang and He 1985). The gigantopterids probably represent tropical woody climbers, carried to the site of deposition by streams or winds (Yao 1983). The brachiopod *Lingula* and the bivalves *B. ceratophaga*, *Stuchburia* sp. and *V.* aff. *yunnanensis* are all euryhaline forms, which lived in shallow marine settings. These floral and faunal characters, along with the lithological characteristics, suggests deposition in a nearshore marine environment, with possible repeated deepening cycles. This high-salinity environment may be largely responsible for the relative scarcity of specimens and their general incompleteness, as such shallow water fully marine faunas are rarely preserved in the fossil record (Schram 1981; Briggs and Clarkson 1989). It is perhaps due to the highly sclerotized nature of the carapace of *F. bifurcatus* that it is preserved in such high numbers, in comparison with *T. asiaticus*. There is considerable generic (*Sphenophyllum*, *Pecopteris*, *Sphenopteris* and *Asterophyllites*) and some specific overlap (*A. longifolius*) between this south-east Chinese flora and that of the Late Carboniferous Mazon Creek Essex assemblage, which has been interpreted as a nearshore marine fauna (Janssen 1965; Pfefferkorn 1979; Schram 1979b). Whilst not closely related geologically during the Permian (Scotese and McKerrow 1990; Ziegler *et al.*, pers. comm.), southern China and continental southern North America were both located near the equator and probably shared tropical environments, which might account for the similar floras.

The single specimen of *F. bifurcatus* from the Lower Permian at Xihushan, Fujian Province was found in dark grey mudstones, with no associated faunal or floral elements. There is a lack of data for this section, due to little collecting having been done. Based on its lithology, this unit is assumed to have been deposited in a coastal marine environment, similar to that inferred for the better known Lower Permian at Changta, Xiangshuping.

A further single specimen of *F. bifurcatus* was collected from an exposure of the Upper Permian at Shitangpu, Hunan Province where the Lungtan Formation is composed of yellowish to dark grey thin-bedded mudstone. It also contains brachiopods (*Spinomarginifera pseudosintanensis*, *Spinomarginifera* sp., *Leptodus tenuis*, *Martinia* sp., *Punctospirifer* sp., *Oldhamina* sp., *Haydenella* sp., and *Gubleria* sp.) and bivalves (*Schizodus* sp., *Palaeoneilo* sp., *Nuculopsis?* sp. and *Stutchburia?* sp.). The absence of terrestrial or freshwater plant material indicates a system isolated from freshwater runoff. The relative abundance of brachiopods, seemingly preserved *in situ*, suggests a quiet marine environment, as does the presence of exclusively fine-grained sediments, which were probably deposited in a nearshore marine or paralic setting, possibly lagoonal or a protected bay (Wang 1985; Zhang 1992).

The occasional presence of carapaces of *F. bifurcatus* and *T. asiaticus* on closely associated bedding planes suggests that these two species lived in the same or closely associated communities. It is difficult to establish their rôle within these communities, however, as their preservation is insufficient to discern such features as mouthpart anatomy and thus insight into feeding type. These eumalacostracans may represent low-level carnivores, as suggested for seemingly similar forms by Schram (1981), but only the collection and description of further material, with better or new morphological details, can answer this question.

Palaeobiogeography

The placement of these new Chinese taxa into the order Pygocephalomorpha presents some new and difficult questions about Palaeozoic palaeobiogeography. Based on this order alone, there is evidently some palaeobiogeographical relationship between central North America, South America, South Africa, Great Britain, and, tentatively, southern China during the Carboniferous and Permian. However, it is not known whether this is due to similar ecological conditions, or to a true biogeographical connection. Whilst Permian maps (e.g. Scotese and McKerrow 1990) show similar latitudinal positions for several areas in which pygocephalomorphs occur (i.e. North America, Great Britain), there is no physical connection between these regions and the land masses destined to make up China. However, the same can also be said for the taxa found in such areas as South Africa and Brazil, which were not closely related palaeogeographically to North America and Great Britain. Thus, the question of historical biogeography for the order Pygocephalomorpha is a difficult one, regardless of the taxonomic position of the tylocaridids.

One possibly important trend can be seen in the temporal distribution of the pygocephalomorphs. All of the 11 known Carboniferous species occur in close association with Laurentia. Conversely, of the six known Permian species, five have a Gondwanan distribution (the exception being *Mamayocaris jepseni*, which is Laurentian in origin). Thus, there was a general shift in the distribution of the pygocephalomorphs from the Laurentian to the Gondwanan coastal margins over the Carboniferous to the Permian, with the exception of isolated populations which remained in Laurentian waters throughout the Permian. This concurs with the observations of Schram (1977), who discussed malacostracan crustacean distributions during the Palaeozoic and the Triassic. He suggested a restriction to Laurentian waters during the Late Palaeozoic for the malacostracans, followed by an expansion of their distribution to other parts of the world with the formation of the Pangaeian supercontinent during the Permian. The new information provided by the tylocaridid pygocephalomorphs clearly supports this observation. It is difficult to draw further conclusions about Palaeozoic palaeobiogeography, especially with respect to the pygocephalomorph crustaceans, from the data as it currently stands.

The same biogeographical problems exist, however, in the alternative hypothesis, in which the tylocaridids might be members of the Lophogastrida rather than Pygocephalomorpha. Little is known about the fossil record of the lophogastrids with the exception of the Carboniferous species *Peachocaris strongi* from North America and the Triassic species *Schimperella beneckeii* from Alsace, France. Thus, the same problematical issue arises: trying to draw connections between the closely related North American and European regions to the distant Chinese land masses.